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RESULTS OF THE ARCHBOLD EXPEDITIONS. NO. 57

A FIELD STUDY OF HOMING IN THE CAROLINA TOAD

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INTRODUCTION

Laboratory experiments have demonstrated that frogs, toads, and salamanders are able to learn how to find their way through mazes (Yerkes, 1903; Buytendijk, 1918). Breder (1925) found that males of a Panamanian tree frog returned on successive nights to the mud basins constructed to care for the eggs, and many other field observations indicate that both frogs and toads, in contrast to most salamanders, return to accustomed places of hiding after nocturnal foraging. McAtee (1921) reports that a bullfrog, when carried a quarter of a mile over land, returned to the home site. The earliest efforts to carry out homing experiments with frogs and toads under field conditions appear to be those of Franz (1927) in Europe and those of Breder, Breder, and Redmond (1927) in New York and New Jersey. More recently Nichols (1937) has reported preliminary studies of the movements of toads, mostly *Bufo woodhousii fowleri*, in eastern United States, and Raney (1940) has included some data on homing in the bullfrog in his account of the normal summer movements of the species, observed at Rensselaerville, New York.

The two experiments described below were carried out with the Carolina toad, *Bufo t. terrestris* (fig. 1), at the Archbold Biological Station in central Florida. Approximately a dozen species of tailless amphibians were observed in the vicinity of the Station, but the Carolina toad, because of its relative abundance and the ease with which it could be seen and caught, was selected for the work. The property on which the Station is located has been mapped in considerable detail; hence it was a simple matter to record with accuracy the points of release.

Various means of marking frogs for future identification have been devised. Breder, Breder, and Redmond (*supra cit.*) used waterproof paper tags attached around the waist with string. Numbers on the tags could often be read without disturbing the amphibians. Raney (*supra cit.*) found the jaw tag method to be entirely satisfactory, and he believes that the use of metal tags is superior to other methods of tagging, especially for long-term studies. Because our investigations were undertaken when an opportunity fortuitously arose, no tags were immediately available. Consequently the toe clipping method was used. This requires time, patience, and considerable care, and there are other minor disadvantages. However, the technique was found to be adequate for the work.

REGION AND TERRAIN

The Archbold Biological Station is located in the middle of the peninsula of Florida, approximately 7 miles south of the town of Lake Placid in Highlands County. Red Hill, which rises to an elevation of 222.2 feet above sea level at the eastern edge of the Station property, marks the southern limit of the Highlands Ridge of central Florida. More than a square mile of land, mostly covered with scrub forest,

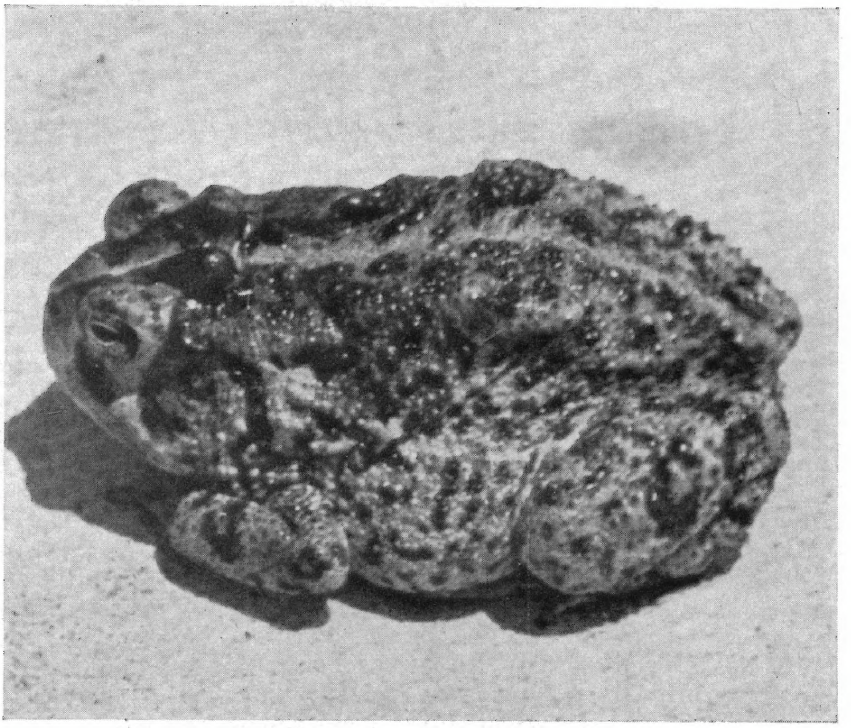

Fig. 1. The Carolina toad, *Bufo terrestris terrestris* (Bonnaterre), an adult female 90 mm. in body length. The knobs at the rear of the cranial crests are most prominent in large females, less so in males, and absent from juveniles; hence the size of the knobs appears to be dependent upon growth factors. This toad, the one used in experiments, ranges throughout Florida and, on the coastal plain, northward to southeastern Virginia, and westward to Louisiana and Arkansas. Along the northern limit of its range it intergrades with *Bufo terrestris americanus*.

has been maintained in semi-virgin condition for a number of years, although a highway traverses the scrub, and a drainage ditch has been dug, as indicated on the accompanying map (fig. 2). The buildings housing laboratories and personnel are all located on the western side of the property in the vicinity of a large paved plaza, approximately 70 yards wide and 100 yards long. West of the Station a small drainage ditch separates the main buildings from railroad tracks, and beyond the tracks the land, virtually denuded of the forest cover by lumbering operations and burned over annually when the grass is dry, is sparsely covered with patches of scrub palmetto with vestiges of small hardwood hammocks, and occasional shallow ponds. This land is relatively flat, although there is a gentle slope toward the Station so that the runoff from the ground flows toward the Station. Water collects in pools after heavy rains (see figs. 3 and 4) and flows under the railroad tracks via culverts to the drainage ditch that in turn carries the water northward into a small pond known as Lake Annie. Photographs (figs. 5 to 7) taken from the top of a large water tower a few yards east of the plaza depict the land and the plaza where toads were collected and released.

The terrain throughout the region is sandy, and the water level during the rainy season is not far below the surface. Drainage ditches near the lower levels on the land owned by the Station contain running water almost constantly. The ditch between the railroad tracks and the Station is relatively shallow since only the plants, mostly grasses and weeds, that grow in it prevent the sides from caving. The drainage ditch on the east side of the plaza is

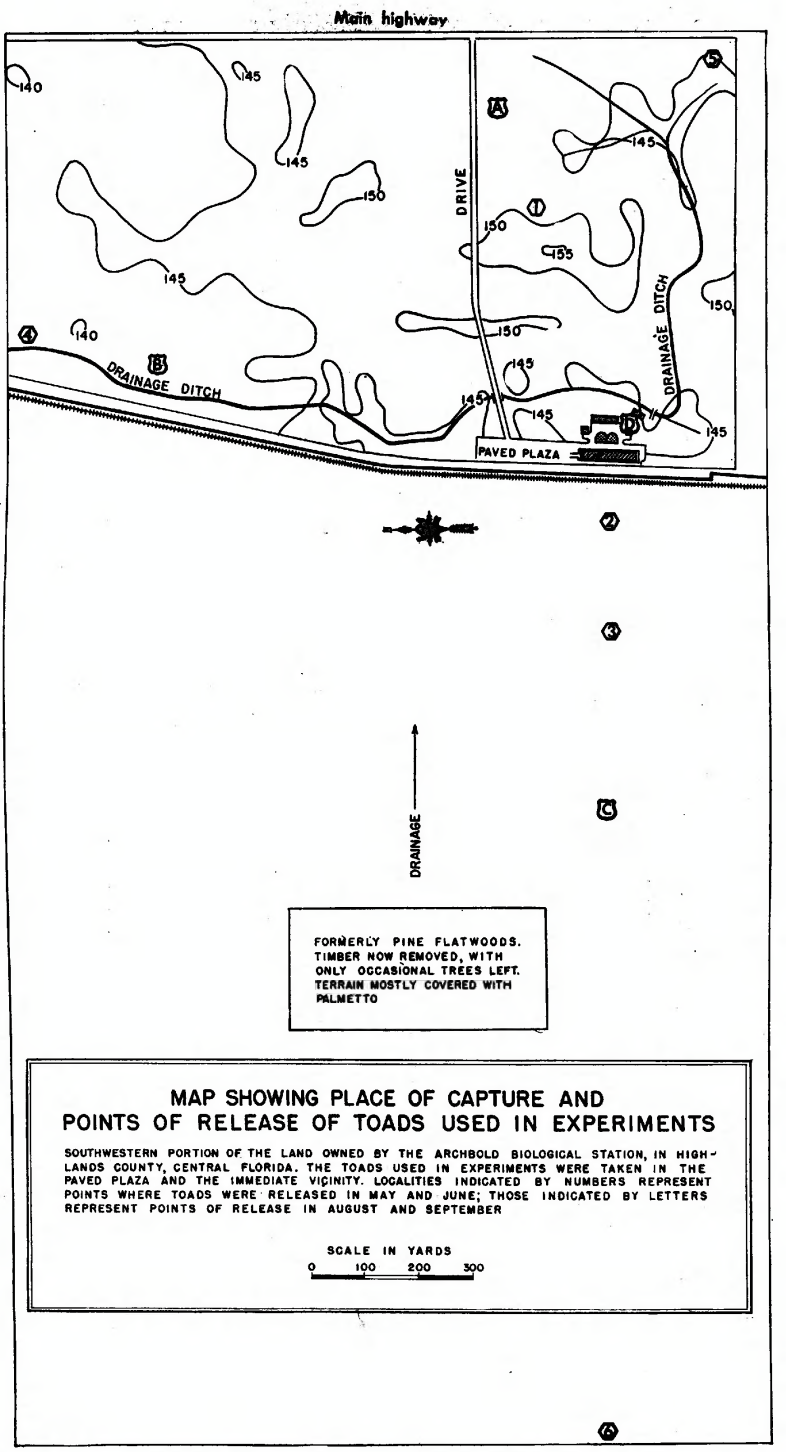

Fig. 2. Map of the region where experiments were conducted. The area with contours shown is part of the semi-virgin area included in the Archbold Biological Station property, and inhabited by *Bufo t. terrestris*. The area (without contours shown) to the west of the drainage ditch and the railroad tracks has been cleared, with virtually all of the timber removed. Smaller plants are burned annually, and the region did not appear to be inhabited by *B. t. terrestris*, although temporary pools immediately west of the Station were used as breeding sites.

4 or 5 feet deep, more nearly V-shaped in cross section, and faced with porous bricks. There are bridges at infrequent intervals (see map), a fact of some interest because toads released east of the plaza presumably found it necessary to cross the deeper drainage ditch in order to return. Not far south of the plaza there is a small truck garden, and after rains toads were particularly abundant along the road immediately west of it. Three houses in the vicinity of the garden, with small poultry yards, lawns, and water hydrants, seemingly make that portion of the premises a suitable haven for numbers of toads; over half of those used in experiments were taken at this end of the area wherein toads were collected.

RAINFALL

The mean annual rainfall for Highlands County has been recorded by the United States Weather Bureau 25 miles north of the Station at Avon Park, as 52.12 inches. Means for each month are reported (Kincer, 1941, p. 809) as follows:

January	2.18 inches
February	2.49
March	2.25
April	2.56
May	4.58
June	8.12
July	8.06
August	7.60
September	6.78
October	3.97
November	1.70
December	1.83

However, the precipitation at the Archbold Biological Station is not likely to be identical with that at Avon Park. Moreover, the rainfall fluctuates from year to year. Because the activities of toads are governed to a large extent by the availability of surface moisture it is pertinent to record here the daily rainfall during the period between May 26 and September 14, 1944, when experiments were in progress. The following data (table 1) were recorded by the Station on a standard rain gauge located at the edge of the plaza.

TABLE 1

RAINFALL AT ARCHBOLD BIOLOGICAL STATION, RED HILL, HIGHLANDS COUNTY, FLORIDA, 1944
(In inches previous 24 hours.)

Date	May	June	July	Aug.	Sept.
1		—	.10	.05	.04
2		—	.13	—	—
3		—	.19	.49	—
4		—	—	.04	—
5		—	—	.51	—
6		.10	—	—	.04
7		.52	—	—	—
8	.11	3.15	—	—	—
9	—	.27	—	—	.57
10	—	1.55	—	.17	.28
11	—	.92	.43	.50	.07
12	—	.38	.40	—	—
13	—	.02	—	.44	—
14	—	.13	—	—	—
15	—	—	—	.59	—
16	.84	—	—	—	
17	—	.02	.025	1.01	
18	.10	—	—	—	
19	.52	—	.35	.20	
20	—	—	.03	—	
21	—	1.35	.60	.39	
22	—	—	.51	.40	
23	—	—	.01	.05	
24	—	—	.05	.85	
25	1.09	—	.45	—	
26	—	—	.44	—	
27	—	.17	.04	.34	
28	—	—	.18	2.39	
29	—	—	.80	.83	
30	—	.12	.02	5.03	
31	.01		.14	.04	

Air temperatures with both wet and dry bulb thermometers were recorded at the Station with a Bristol recorder, but their bearing on the movements of toads was of importance only under extreme conditions. Therefore detailed data have been omitted. Moisture is constantly being lost through the skin, cooling the toad to such an extent that its temperature is approximately 2° C. above that of a wet bulb thermometer when the relative humidity is much below 100 per cent. Hence the body temperature of a toad is partly dependent upon the humidity, but it will suffice to say that nocturnal temperatures recorded on the wet bulb thermometer were well within the limits of the activity range of toads throughout the experiment. *Bufo t. terrestris* was breeding whenever suitable rains occurred during the time that the experiments were in progress, and one or more individuals were abroad every night in the area where the toads used were captured.

METHODS

Other investigators have usually attempted to record more or less precisely where individual frogs or toads were found prior to being marked and carried elsewhere for release. In the experiments described herein toads were collected only within a limited area and no attempt was made to note the exact spot where each was first seen. The area chosen was that encompassed by the paved plaza and the adjacent buildings at the Archbold Biological Station. All individuals marked and released were taken within an area approximately 400 yards long and 100 yards wide (see map, fig. 2).

Because toads are essentially nocturnal in their activities all collecting was done between dusk and midnight, usually between the hours of 8:00 P.M. and 1:00 A.M. As far as possible the identical route around the periphery of the plaza was covered twice each evening. Toads were most often encountered in the open, along roads, on lawns, or on the paved plaza where they were easily seen when the beam of a five-celled flashlight strapped on the forehead was directed toward them. Often the "eye-shine" would disclose a toad at distances of 50 feet or more. When first captured toads were dropped into a wet cotton sack. At the conclusion of the evening's collecting they were carried to a large wooden sink in the laboratory where they were retained until they could be marked and released. Sometimes it was necessary to wait as long as four days before a sufficiently large lot could be assembled to make it worth while to release them.

Marking for future identification was accomplished by excising toes, as noted above. Digits were clipped with a pair of scissors, from one to three being removed as close to the base as possible, without cutting the web of the hind feet. No more than one toe was removed from any foot. Serious discomfort to the toads was not manifest as a result of the wounds; the specimens with clipped toes were apparently as normal in behavior as those not marked. On specimens retaken a few days after release, the wound had nearly healed and those recaptured after two months were readily identified even though in a few instances there was partial regeneration of digits. Under a dissecting microscope with light transmitted from below, it was easy to detect excised toes even when partial regeneration had occurred because bone was not present in the regenerated portion.

Extra digits occurred on two of the 444 toads marked, but none lacking toes was discovered prior to the date when toads with excised digits had been liberated. Two toads of the first 200 captured lacked one fore limb, and these were rejected for use in experiments. Few serious abnormalities or deformities were noted except for one specimen that lacked a functional eye on the right side, apparently as a result of injury.

When a sufficiently large number of toads had accumulated, digits were excised in various combinations. Because there are but four toes on the front feet, the toes on the hind feet were used for digits in the numbering system that was devised in advance in order to avoid any possibility of duplicating numbers. With this system and the series used it was not necessary to clip more than one toe on each limb. For example, the last toad marked in a series numbered consecutively was No. 250; on this one the left front foot had the fourth toe removed, the third toe was removed from the right hind foot, and the fifth toe was cut from the left hind foot.

Although relatively few toads were seen killed by automobiles on the highway traversing the property, no toads were liberated east of this road, in an effort to eliminate one hazard to which toads might be subject. Little is known concerning the mortality rate of adult toads. Highway casualties are those most frequently seen, but aside from man there are doubtless many other enemies. Ophidian enemies of toads include the hog-nosed snake (*Heterodon contortrix*) and the indigo snake (*Drymarchon corais*), neither of which was at all common in the area where experiments were conducted. To what extent the local mammals and birds prey upon

Figs. 3 and 4. Temporary pools west of the Archbold Biological Station formed late in the season and utilized as a breeding site by *Bufo t. terrestris*.

toads one can only guess. Probably a few of the toads marked and liberated never survived even though only healthy toads between the sizes of 38 mm. and 90 mm. in body length were liberated. The vast majority of these were males; scarcely 25 per cent were females in the samples in which the sex was recorded.

FIRST EXPERIMENT

PURPOSE: The work was undertaken with the hope that answers or partial answers could be obtained for some of the questions involved in homing in toads. For examples: Is it easier for a toad to find its way home when released at a distance of 100 yards than it is for a toad to return when released a mile from the home site? In other words, aside from the hazards that beset normal travel, is there a negative correlation between the distance a toad is removed and the number of chances it has of returning? Does a toad liberated in an unsuitable habitat return to the home site as readily as one liberated in a habitat that is suitable for the species? Finally, what is the maximum distance that a toad is capable of traversing in order to return? These are the principal questions for which answers were sought.

PROCEDURE: Because toads are most active during or immediately after rains they can be taken in large numbers only at infrequent intervals. Thus it was impractical to release toads at regular intervals or in lots of similar sizes. Until the afternoon of May 25, following a storm that brought 1.09 inches of rain (see table 1), relatively few toads were seen. After this storm 19 specimens were taken. These were marked as described above and liberated the following evening at a distance of 450 yards east of the plaza, in an area with dense vegetation where toads of the same species were present but not abundant. The next lot, comprising only 13 toads, was liberated on May 29 at a distance of 100 yards from the plaza. The point of release was in the cleared area west of the Station where no *Bufo t. terrestris* had been seen previously. On the evening of June 1 a slightly larger lot composed of 15 individuals was liberated in the same direction, in the same sort of terrain, at a distance of 300 yards. A slight rain on May 31 (.01 inch) brought forth a few more toads than it was possible to secure during the dry interval between May 28 and May 30, and 18 toads were available on June 1. These were liberated at a distance of 850 yards to the north at the edge of the Station property, and not far from a small pond where toads of the same species were moderately abundant. No rain occurred after this lot had been liberated until June 6 when 0.10 inch of rain fell, and the following day there was a second storm that brought 0.52 inch. Toads were abundant in the plaza on these nights, particularly on the second night, and 92 individuals, including five that had been recaptured, were liberated on the night of June 8 at a distance of 750 yards to the east of the plaza, at a point near the head of one branch of the drainage ditch, but at the same elevation as the plaza. *Bufo terrestris* had been seen previously, at the place of liberation, and a fair population was known to exist immediately to the south beyond the Biological Station property where a farm house and gardens were located. A storm on the night of June 8 produced a heavy rainfall, 3.15 inches, but toads were not quite so abundant as they had been the previous night, possibly because many that were active the two preceding nights had been removed. However, 43 individuals were secured, and after they had been marked the following day they were taken to a point 1 mile west of the plaza and liberated late in the afternoon.

The data for the six lots of toads liberated are shown in table 2. In summary, three lots of toads were liberated at distances of 100, 300, and 1760 yards west of the plaza in the timbered area that is burned over annually; since toads of this species were never encountered far beyond the drainage ditch, the area presumably represents an unsuitable habitat for *Bufo t. terrestris*. One lot of toads was liberated to the north at a distance of 850 yards, and

Fig. 5. View from top of water tower, showing the southwest corner of the property owned by the Archbold Biological Station, and portions of cleared area west of the railroad tracks. The majority of the toads used in experiments were taken in the area in the center of the picture.

Fig. 6. View from the water tower to the west, with the buildings of the Archbold Biological Station in the foreground. The pool at the left was the principal breeding site for the toads used in experiments. Toads in Lot 6 were liberated 1 mile west of the buildings in the cleared area.

two lots were turned loose respectively 450 and 750 yards east of the plaza, in all cases in places where toads of the same species occurred.

Following the release of the first lot of toads on the evening of May 26, a search of the plaza was made every night until June 15 when the work was interrupted. No toads were taken again until the evening of August 15 when work was resumed. Between the dates of August 15 and September 14, after the two month lapse, all toads that could be located in the plaza and the immediate vicinity were captured, and a record was kept of all marked, as well as of unmarked, individuals that were taken.

RESULTS: Of 200 toads marked and liberated at various distances from the plaza, a total of 53, or 26.5 per cent, were subsequently retaken. Of the 53 only 20, or 10 per cent of the total, were recovered during the first stage of the experiment in May and June. The other 33 individuals were all taken at the home site when collecting was resumed after a lapse of two months. No fewer than 20 of the 33 were taken on a single night, August 28, after 2.39 inches of rain; on the afternoon of that day 196 toads were located in or near the plaza, and 21 of the 196 were marked toads that had been liberated in May and June.

Of the two lots liberated east of the plaza, 36.8 per cent of those liberated at a distance of 450 yards were recovered in the plaza, but only 20.6 per cent of the lot removed 750 yards were seen again at the home site. Of the lot taken 850 yards to the north, 16.6 per cent were recovered. Nearly 54 per cent of 13 toads taken 100 yards to the west were retaken, 60 per cent of a second lot taken 300 yards to the west were later found in the plaza, but of 43 taken to a point of liberation a mile from the plaza only 18.6 per cent are known to have returned to the home site.

One toad taken 300 yards to the west and one toad liberated 850 yards to the north were back at the plaza the evening of the day following their release. The maximum time intervening between release and recapture was recorded for two taken after being released 96 and 97 days, respectively. These data are summarized in table 2, along with other pertinent information, and the exact place where each of the six lots (indicated by number) in this table were liberated is shown on the accompanying map (fig. 2).

CONCLUSIONS: The data presented above are not sufficiently extensive for entirely satisfactory conclusions to be drawn. Because only six lots of toads were liberated in three directions the data are inadequate for extended statistical treatment. Moreover, it is difficult to evaluate the effects of changes in the weather. The activities of toads are governed to a large extent by the rainfall. As may be seen in table 3 below, wherein the number of toads taken over a period of two weeks is plotted separately for each night and the rainfall is indicated in the adjacent column, the numbers of toads seen in the same area in the course of several evenings are correlated with the rainfall the previous 24 hours, although the effects of a heavy rain may persist for two or three days. Additional data not included in table 3 will serve to explain the total recorded for September 1. On the night of August 28 a total of 196 toads, the maximum number taken on a single evening, was obtained in the plaza and the immediate vicinity after 2.39 inches of rain had fallen during the day. The storm was almost continuous, and notwithstanding the removal of 196 toads, 34 were taken the next night after 0.83 inch, 25 toads were taken on the night of August 30 after 5.03 inches of rain, and 23 on August 31 following 0.04 inch. The reduction in numbers on August 31, despite the heavy rainfall, is undoubtedly due largely to the quantity of toads removed from the area on the two previous nights. But on September 1, when there was only a trace of rain, 15 toads were taken, 10 of which were individuals not previously seen. Beginning on September 1 there was a steady decline in the numbers of toads seen on successive nights until September 6 when there was an abrupt increase following 0.04 inch of rain. After a decline in numbers during two days when only a trace of rain fell, there was a sharp increase on Sep-

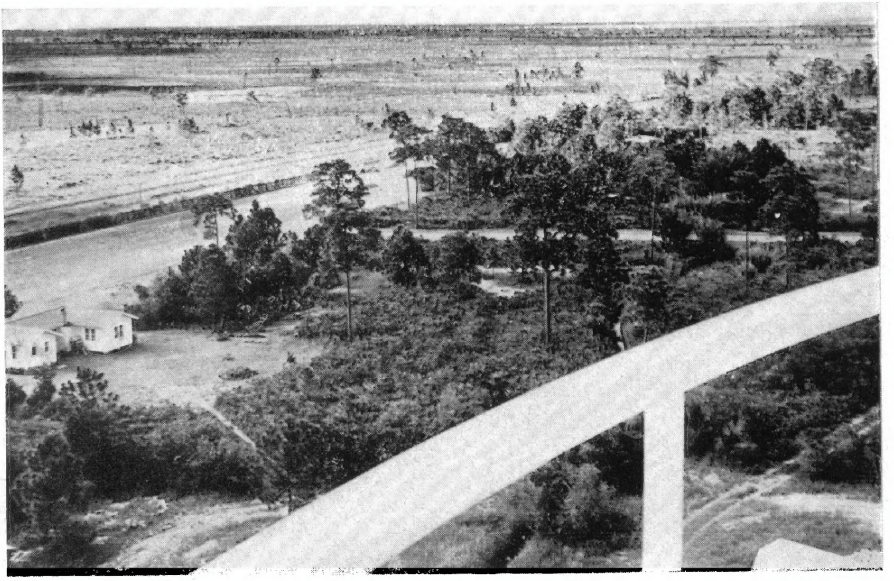

Fig. 7. View from the water tower to the northwest, showing the line of demarcation between the Archbold Biological Station and the cleared area to the west. The body of water near the horizon in the upper right-hand corner is Lake Childs.

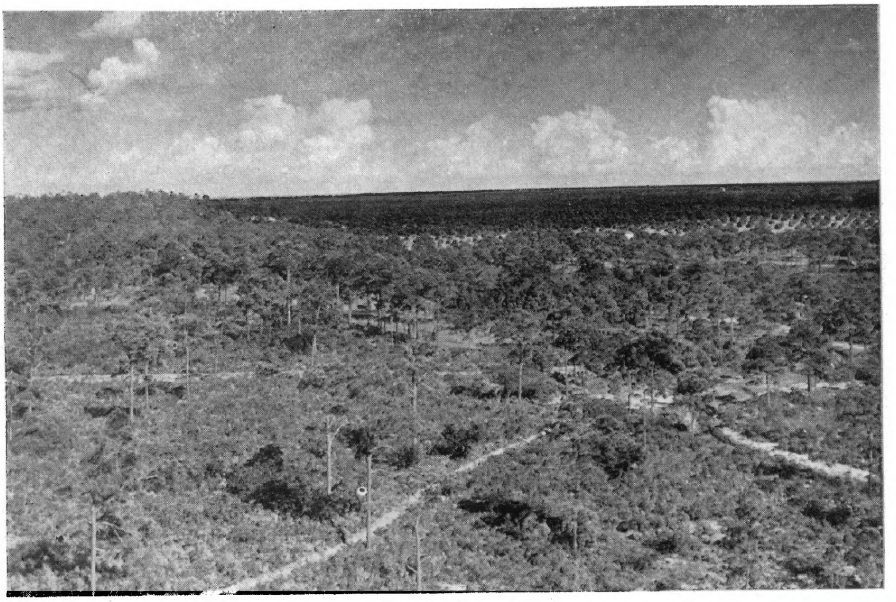

Fig. 8. View from the water tower to the east, with semi-virgin area in the foreground, orange groves at the upper right, and Red Hill at the upper left. Red Hill marks the southern end of the Highlands Ridge of central Florida.

tember 9 when 11 toads were captured after 0.57 inch of rain. These figures provide only a rough approximation inasmuch as the local population was fluctuating in numbers owing to collections made every night as well as to the return after August 31 of many of the 244 toads removed from the home site. Also the figures in column E of table 3 include only toads not previously seen. These data do make it plain that toads are abroad in greater numbers during and immediately after periods of precipitation.

Evaluation of homing data is complicated by weather factors to the extent that we do not know whether a toad often attempts to travel long distances on dry evenings. And if a toad does not try to return to the home site immediately after its release, what is the effect of its being hand one toad released 300 yards to the west, and one toad taken 850 yards to the north were each back in the plaza the night following their release. It is particularly noteworthy that the individual that traveled 850 yards within 24 hours did so on a night (June 6) when there was a fair amount of rain, 0.52 inch being recorded for the previous 25 hours the next evening. The only toad that reappeared in the plaza within 24 hours after release during a dry interval was one removed only 300 yards to the west. It is of some interest to ascertain how rapidly an adult toad can travel, and 850 yards in 24 hours is the maximum that can be proved with the data secured at the Archbold Biological Station. Aside from this information the data tabulated in the right-hand column of table 2 are of incidental interest,

TABLE 2

SUMMARY OF DATA FOR TOADS RELEASED IN MAY AND JUNE, 1944

Lot	Number Released	Date	Distance Removed	Direction	Recoveries No.	Recoveries Per Cent	Time in Days, Release to Capture
1	19	5/26	450 yds.	East	7	36.8	9 to 93
2	13	5/29	100 yds.	West	7	53.8	2 to 86
3	15	6/1	300 yds.	West	9	60.0	1 to 88
4	18	6/6	850 yds.	North	3	16.6	1 to 84
5	92	6/8	750 yds.	East	19	20.6	6 to 96
6	43	6/9	1760 yds.	West	8	18.6	80 to 97
Totals:	200 released				53	(26.5%) recovered	

prevented from heading homeward? Does it always find suitable shelter, and if it is delayed in its departure for home does the delay diminish any original stimulus or interfere with the toad's ability to return? These are questions that cannot be answered at present, and yet they have some bearing on the interpretation of the data presented above.

A few toads were discovered in and around the plaza every evening, but some of these had access to water from lawn sprinklers, dripping spiggots, or other domestic sources. Following the liberation of the first lot of toads on May 26 there was no rain until May 31, and no heavy rain until June 7. One toad was discovered in the plaza on June 4, nine days after being released. It cannot be assumed, of course, that this toad was found the night of its arrival. On the other and for this reason only the maximum and minimum number of days that elapsed between release and recovery are recorded.

Even though it was demonstrated that an adult *Bufo t. terrestris* can travel 850 yards in 24 hours (and probably in less time since the species was not active during the day), it is not known whether the toads that succeed in returning home do so by the most direct route, unless fortuitously, or whether most of them wander about before heading in the proper direction. Time is undoubtedly a factor of some importance in homing experiments with toads, but the 200 toads released in May and June should have had ample opportunity to return to the home site during the three-month period that elapsed between their release and the last day when a search of the plaza could be made. Although those released on May 26 were provided with more time

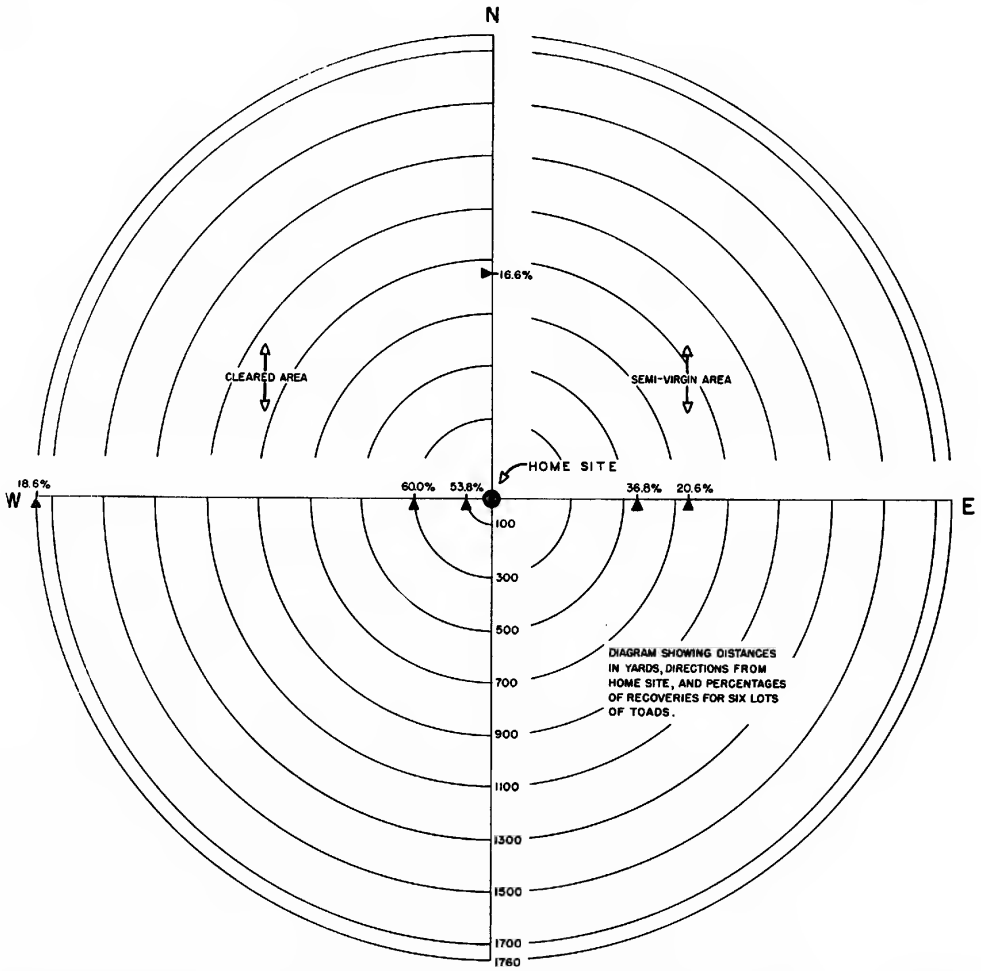

Fig. 9. Diagram showing percentages of recoveries obtained in first experiment. The area west of the vertical line represents the cleared territory that appeared to be uninhabited by *Bufo t. terrestris;* the vertical line represents the edge of the Archbold Biological Station property, and the entire area east of the line is in a semi-virgin state and inhabited by *B. t. terrestris.*

than those liberated on June 9, the results obtained for individual lots can be compared with some assurance that the percentages of each lot represent comparable, if not entirely accurate, samples of the toads in each lot that actually returned to the home site.

Because the individual groups of toads marked and liberated were taken from the home site in three main directions and liberated in different sorts of habitat, data from table 2 have been plotted in a diagram (fig. 9) for clarification. In this diagram it may be noted that the percentages of toads recaptured from two lots released to the east of the plaza indicate that nearly twice as many toads managed to return from a distance of 450 yards as returned from a distance of 750 yards. Still fewer toads were recovered from a third lot released in the same sort of habitat 850 yards to the north. Of the toads released to the west, in an unsuitable habitat, a somewhat larger percentage of the lot released at a distance of 300 yards were recovered than in the lot released at 100 yards, in each case over 50 per cent. However, of the lot released a mile away in the same direction, only 18.6 per cent were subsequently seen in the plaza. The data are

comparable only when lots released in similar habitats are considered. Under these conditions a negative correlation exists between the distance a toad is removed and the toad's chances of returning. Inasmuch as nearly one-fifth of the toads removed 1 mile from the home site were recovered, it is plain that under favorable circumstances toads can return from distances exceeding a mile.

It is also evident that the nature of the terrain or the suitability of the habitat may have some bearing on the toad's homing ability. Only 16.6 per cent of the toads taken 850 yards to the north and only 20.6 per cent of those taken 750 yards to the east were recovered, whereas nearly the same percentage (18.6) was recovered from the lot taken 1760 yards to the west. The localities of release to the north and to the east were known to be inhabited by, and hence represented suitable habitats for, *Bufo t. terrestris;* the area west of the Biological Station evidently was not a suitable habitat for *terrestris*. Thus, proportionately fewer toads returned from the suitable habitat than returned from the unsuitable one, but it cannot be stated whether the absence of dense vegetation in the cleared area made it easier for toads to find their way home from the west, or whether new territory was simply adopted by the toads liberated in the east. Nor is it possible to evaluate the relative importance of predators in the two types of terrain. Conceivably enemies of toads are more abundant in the places frequented by these salientians, but predation is probably a minor factor in this sort of experiment.

SECOND EXPERIMENT

PURPOSE: There is no satisfactory means of determining precisely how many toads return to the home site, because it is manifestly impossible to locate every individual that succeeds in returning. For this reason it is desirable to devise some method of estimating the total number of returns. This can be done, in theory at least, by introducing a control group. By marking a number of toads and liberating them at the home site it is possible to calculate the total number of individuals in a given area (see Dice, 1941, for a discussion of methods employed by mammalogists). The ratio of the number of recoveries to the total number released should be the same as the ratio of the number released to the total population. This involves a second assumption, based on evidence cited below, that toads released where taken tend to remain in the vicinity. Application of the same reasoning makes it possible to estimate the number of toads that return by comparing the percentages of recoveries in a lot liberated at the home site with the percentages of lots liberated away from home. The purpose of the second experiment, therefore, was to gain some estimate of the actual number of toads that returned when lots of similar size were liberated in three cardinal directions.

PROCEDURE: Heavy rains during the latter part of August (see table 1) made it possible to assemble a large number of toads in the plaza. Within three days, August 28, 29, and 30, a total of 244 individuals were taken. This assemblage was divided into four lots, each comprising 61 individuals. For convenience in tabulating the results and in mapping the points of release (fig. 2) these lots are designated with capital letters. To permit ready identification all toads in each lot were given the same mark, instead of individual marks for each toad, as in the previous experiment.

Late in the afternoon on August 31 three of the individual lots were taken to points of release 700 yards from the plaza. (See table 3.) Those in Lot A were liberated 700 yards east of the plaza in pine flatwoods. The same number of toads, in Lot B, were carried to a point of release 700 yards north of the plaza on the edge of the semi-virgin pine flatwoods, immediately to the east of the burned-over area. Those in Lot C were taken 700 yards west of the plaza, into the burned-over area. The toads comprising Lot D were liberated

at the eastern edge of the plaza near the center of the area considered to be the home site. All toads were carried in wet sacks to the four points of release within an hour's time, those in Lot D being liberated last. Each lot comprised not only the same number of toads, but each was of approximately the same composition, those in each lot being selected at random from the 244 toads on hand.

Beginning on the night of September 1, for a two-week period terminating on the night of September 14, a search of the plaza was conducted every evening. As in the previous experiment, a regular route reaching all portions of the area where collecting had been done in and around the plaza was covered twice each evening between the hours of dusk and midnight. All toads seen were examined, but only those in the four lots liberated on August 31 were collected. Unmarked toads, that is, toads not previously seen in or around the plaza, were collected and liberated where they were taken, immediately after they had been given a special mark of identification. This was done in order to avoid counting them on subsequent nights when they were found again. Thus in table 3, column E labeled "Unmarked" includes only the "new" toads found on successive nights. The number of toads recovered from each of the marked lots was similarly recorded.

RESULTS: Toads from each of the four lots liberated on the afternoon of August 31 were recoverd on the evening of September 1; one had returned from the east, two from the north, and one from the west, whereas only one of the 61 individuals liberated at the home site was recovered. There was a slight rain, officially a "trace" that night, and 10 unmarked toads were found. On the following night, when there was no rain at all, one toad from the east, two more from the north, and three from the lot released at the home site were recovered; 10 unmarked toads were seen. The data for the two-week period are summarized in table 3 wherein it may be observed that by midnight on the four-

TABLE 3

SEPTEMBER EXPERIMENT.
FOUR LOTS OF TOADS, EACH COMPOSED OF 61 INDIVIDUALS MARKED AND RELEASED ON EVENING OF AUGUST 31, AS FOLLOWS:
Lot A 700 yards east of plaza in pine flatwoods
Lot B 700 yards north of plaza at edge of pine flatwoods
Lot C 700 yards west of plaza in cleared area
Lot D, control group, in plaza at site of capture
(Column E lists unmarked specimens not taken previously)

Date in September	Toads Taken in Plaza Following Release					Totals	Rainfall
	A From the East	B From the North	C From the West	D Released in Plaza	E Unmarked		
1	1	2	1	1	10	15	Trace
2	1	2	0	3	4	10	None
3	0	0	0	2	3	5	None
4	0	0	0	0	4	4	None
5	0	0	0	0	1	1	Trace
6	2	0	1	1	2	6	.04 in.
7	0	0	0	0	2	2	None
8	0	0	0	0	1	1	Trace
9	0	1	1	1	8	11	.57 in.
10	0	1	0	1	3	5	.28 in.
11	0	0	0	1	8	9	.07 in.
12	1	0	0	0	3	4	None
13	0	0	1	0	4	5	None
14	0	0	0	0	3	3	None
Totals	5	6	4	10	56	81	

teenth day five toads from the east, six from the north, four from the west, and 10 from the lot liberated at the home site had been recovered, whereas 56 previously unmarked toads were taken in the same area during the period.

One other observation is worth recording: Although the toads listed in column E of table 3 had obviously not been seen around the plaza until they were captured and marked, after September 1 many of them were recovered several times subsequently. Unfortunately the same identifying mark was given to all toads collected during the period so that in many cases the precise identity of an individual was not certain. However, when a freshly marked toad was found in approximately the same place night after night it is a safe assumption that in most cases it was the same toad. In one instance it was definite. On the night of August 31 a toad was found sitting on the walk near one of the buildings in the area. Examination disclosed the fact that on the right foot the third toe was abnormally long and coalesced with the fourth toe. Thus the individual, even without clipping toes, was readily identified on later nights. Although it was always picked up, examined, and then tossed 10 to 20 feet away into a patch of scrub palmetto, the toad was found night after night stationed on the narrow walk, and never more than a yard away from the spot where it was seen on the first night. From the night of August 31 until September 14 the toad was absent from its accustomed place on only two evenings.

Conclusions: Inasmuch as toads tend to remain within a limited area, and only 10 of the 61 individuals liberated at the home site were recovered within a two-week period, it may be assumed that only 16.6 per cent of all toads present in the area to which collecting was confined were seen in the course of 14 nights. Toads from the lots liberated to the east, north, and west were recovered in the plaza and the vicinity in approximately equal numbers, five, six, and four, respectively, or on the average five, or 8.6 per cent of each lot. Approximately twice as many were recovered from the lot comprising the same number of individuals liberated at the home site. Thus, if the samples permit a reliable estimate of the actual number of toads from each lot that were present, and the 61 toads liberated at the home site presumably remained there, then in the course of 14 days approximately half as many toads or approximately 30 from each lot, must have returned to the home site from each of three points of release 700 yards distant. These data suggest, therefore, that approximately half of the toads released at a distance of 700 yards managed to return to the home site.

DISCUSSION

The irregular periods of activity and the uncertainty with reference to the movements of toads during the periods when they are abroad make it impossible to arrive at valid estimates of the total number of toads in a given area, or to ascertain how many are using a breeding site. Dice (1941) has discussed the technique employed in the second experiment, outlining his objections to the method when applied to mammal populations, and several of his criticisms can be applied to estimates of toads. When equal numbers of toads taken throughout an area are liberated in various directions, and when the same number of toads is marked and liberated in the same area, the estimate of the number of returns is probably more nearly valid than an estimate of the population.

The number of toads recovered from Lot D liberated at the home site in the second experiment can be compared with the total number of toads found that were previously unmarked. If 10 toads (or 16.6 per cent) of the 61 marked and liberated at the home site were recovered, then 56 unmarked toads taken during the same interval should represent approximately 16.6 per cent of the total active population. On this basis there must have been 336 unmarked toads in the collecting area. This figure doubtless represents only an

estimate of the total number of toads that were abroad or that passed through the territory covered during a two-week period. A total of 200 toads had been marked and liberated at various distances in May and June, and 244 toads had been marked during the second experiment in August and September. Hence there were 444 toads marked and liberated in the vicinity, of which only 68 were seen again in the plaza during the period of the experiments.

It was estimated from the sample liberated in the home territory that approximately half of the toads taken to the points of release in each of three directions had returned. On the other hand, most if not all of the toads liberated at distances of 100 and 300 yards in the earlier experiment supposedly managed to return, even though scarcely more than half of each lot was recovered. But for other distances and directions the ratio of actual returns to the number retaken cannot be estimated. In any event the total number (444) of toads marked, plus the total number (336) of unmarked toads estimated by means of the sampling technique, indicate only that approximately 780 individuals were active in the vicinity of the plaza during the period of time that collecting was carried on. Toads were not only coming and going, aside from the 444 removed for experimental purposes, but those remaining were in hiding part of the time. It seems reasonable to assume, however, that similar percentages of each of the four lots used in the second experiment were abroad at the same time; hence the percentages of recoveries should be reliable indices and the estimates should be valid.

It has been stated that frogs are familiar with the details of their local habitats and that if they stray from their home territory they are able to find their way back even after long periods of time by "making use of land marks to a large extent" (Noble, 1931, pp. 405–406). This view is substantiated in part by the work of Yerkes (1905) and of Franz (1918). The experiments of Yerkes proved that vision as well as kinaesthetic factors were important in the establishment of the labyrinth habit, and that associations persisted for at least a month. Franz found that *Bufo calamita*, with better vision than *Rana temporaria*, had less difficulty finding its way back to an accustomed retreat than the latter species. These laboratory experiments, therefore, point to the possibility that vision, kinaesthetic sense, and memory may each play some role in homing. The information derived from a study of one species unfortunately cannot be applied to problems concerned with another; experiments have demonstrated that various species of Salientia differ greatly, not only in their speed of learning but in their ability to remember. Moreover, the same species of toad that "remembered" a disagreeable morsel and avoided it for only two days acquired useless motor habits that persisted for a number of days (Buytendijk, 1918).

If memory, kinaesthetic sense, or vision is involved in homing it is important to know something of the normal movements of toads. Unfortunately the extent of the wanderings in *Bufo t. terrestris* has not been ascertained. Nichols (1937) reports that a toad, probably *Bufo woodhousii fowleri*, had spontaneously traveled 1400 yards when "not removed" from the home site. Blair (1943) states that in Oklahoma the American toad (*americanus*, placed as a subspecies of *terrestris* by Netting and Goin, 1946) traveled as far as 900 yards within 10 days, although there was the possibility of passive movement by flood waters. Evidently there is much variation in the activities of individual toads, since Blair found others only 45 feet from the original breeding site 15 days after marking them. Blair's data as well as Nichols' are of interest in that they demonstrate the possibility of a toad's being familiar with an area well over a mile wide. Moreover, their data indicate that toads may be somewhat less sedentary than the bullfrog, *Rana catesbeiana*, studied by Raney (1940) who found great variation in the distance that individuals of both sexes as well as juveniles would move. Some bullfrogs moved less than 100 feet throughout the summer, whereas the maximum was only 100 yards. Contrary to inferences that might be drawn

from McAtee's (1921) report, Raney found little evidence of well-developed homing behavior. It would seem possible that the bullfrog's apparent lack of ability to return to a home site is correlated with its disinclination to wander great distances. Data supplied by Breder, Breder, and Redmond (1927) for another frog belie this conclusion. These authors studied the normal summer movements in *Rana clamitans* and found them to be variable but on the whole restricted, although they concluded that "a well developed homing instinct" was present in the species.

It is noteworthy that when toads are removed far from the home site they often make no attempt to return. In order to verify this, 15 toads were transported from the Archbold Biological Station in Florida to Englewood, New Jersey, and liberated in a truck garden. Despite adequate cover, seven were seen the night following their liberation, and on following nights a few others could always be discovered. At least one individual was still living in the truck garden over a month after its liberation. Hamilton (1934, p. 90) reports that nine toads (*B. terrestris americanus*) were carried 4 miles from their home swamp and a year later four of them "apparently year old toads" were taken within a few rods of the point of release. His statement that "apparently no homing instinct was developed at this precocious age" carries the implication that only adult toads are able to return to the home site. Auditory cues may be important in homing, and juveniles would not respond to breeding choruses. However, other vertebrates with restricted powers of locomotion, notably box turtles and some of the sedentary birds, tend to remain where they are liberated if they are carried many miles from home. Thus it is not impossible that when toads fail to recognize any landmarks they too remain where they are liberated. Such negative evidence scarcely proves that toads rely upon familiarity with their surroundings and find their way home by means of visual cues. The few data are suggestive, but they do not rule out the possible significance of auditory cues.

The evidence provided by the first experiment described above points to the complexity of homing behavior. A higher percentage of toads returned that had been released a mile away in unfamiliar territory (as suggested by the absence of the species in the habitat) than returned from a distance of 850 yards over terrain that supposedly might have been known to the toads if their normal movements approximate those of the subspecies *B. t. americanus*. Factors other than familiarity with details in their home range probably are involved, and it can scarcely be postulated that the absence of heavy timber permitted toads a mile distant to identify landmarks at their home site. It would be preferable to assume that a higher percentage of toads liberated in the more agreeable surroundings tended to remain near the point of release because the territory was included in their normal range and hence was familiar. Or, in the negative it might be said that the familiar terrain was not so disturbing as the cleared area west of the Biological Station. An alternative explanation is discussed below.

It is not impossible that toads utilize topographical knowledge in returning to the home site. Cummings (1912) found that European newts (*Triturus*) showed a marked tendency to walk downhill. These newts were able to return to the home site from only short distances, and Cummings concluded that if they wandered from the precincts of their native pool they became lost and probably regained water only by chance. Boulenger (1912) commented on Cummings's paper and suggested that the European toad, *Bufo calamita*, would be a better animal for homing experiments because these toads congregate "from the neighborhood, often from a radius of half a mile. Thither all toads have travelled with remarkable directness, passing other ponds or ditches of which they might avail themselves were it not for the instinct which leads them to select a place offering all guarantees for the successful rearing of their progeny."

Boulenger's statement was accompanied by no data to confirm his conclusions, which may have been based largely upon field observations. Nevertheless his impres-

sion appears to be essentially correct, despite the teleological connotations of his interpretation. Toads evidently congregate at breeding sites, and it is manifest that they come to such sites from several directions, regardless of whether they are traveling uphill or downhill. The area where experiments were conducted in Florida is virtually flat, although a hill rises to the east, beyond the easternmost place of liberation for any lot of toads. Toads taken to the east or to the west, however, were released at points a few feet higher than the plaza (see map, fig. 2). Those taken to the north were a few feet lower than the plaza, but they returned in approximately the same percentages as those released to the east when proportionate distances are taken into account. In the second experiment the returns from the north slightly exceeded those from the east or west. There is little indication, therefore, that the topography, as such, plays any role of importance in toad homing.

The site immediately west of the Archbold Biological Station was the only place within a radius of at least 2 miles where breeding was noted, and presumably all the toads taken there represent one colony. The ditches and pools serve as a sort of center for the colony. Most, if not all, of the toads in the vicinity probably have gone through their metamorphosis at this breeding site. Between breeding periods they presumably scatter, with the major portion going eastward from this center, either into seclusion or to establish a feeding site. It was mentioned that in one instance a toad was found at almost the same spot for 13 nights out of 15, despite the fact that this toad had not been seen previously. Evidently it had adopted the site when first discovered; it could not have been stationed there during the previous two weeks since the area where it was found was searched twice each night. Circumstantial evidence suggests, therefore, that toads remain inactive for prolonged periods, but emerge under suitable weather conditions to breed, or at other times to select feeding stations that are used night after night. Breder, Breder, and Redmond (1927) note that individual green frogs frequently disappear from an accustomed site for a few hours or even several days and cannot be found elsewhere. After they had dredged ponds and made every effort to find such frogs without success, they gained the impression that there was some sort of periodicity in the movements of frogs that caused individuals to "hide away in inaccessable [*sic*] places, possibly after an extra large meal to await the processes of digestion."

What evidence there is suggests that a toad's activities are much like those of the green frog in this respect. Whereas much individual variation is manifest, many toads undoubtedly are not active throughout the summer. Moreover, it may be inferred that individual toads differ considerably in the extent of their wanderings. The data published by Blair and by Nichols indicate that some toads are comparatively stationary while others are traveling long distances. It follows that one toad might be "familiar" with considerably more territory than another. If this is so, and if visual cues play any role in homing, it is conceivable that only those toads return that have not been transported beyond territory previously known to them. This hypothesis would account for the decreasing percentages of recoveries from lots liberated at increasingly greater distances from the home site, but in the same sort of terrain. However, the relatively high percentage of recoveries in the lot liberated in the area not frequented by *terrestris* a mile to the west is not explicable on this basis.

Random radial scattering from the point of release can scarcely account for the toad's ability to return to the home site. The discrepancy between the percentages of returns from the two areas in the first experiment, the cleared area and the semivirgin area, points to some other factor or factors. In the second experiment toads apparently returned from three directions in approximately the same numbers, regardless of the terrain. If the estimate of 50 per cent for actual returns in each of the three lots is valid, radial scattering alone would not account for so many returns, even though it be conceded that the extent

of the territory possibly familiar to the toads used is unknown.

The contrast in the results of the two experiments suggests that a temporal factor is involved. In the first experiment, where three months elapsed before collecting was terminated, the percentage of toads recovered from a point a mile distant in the cleared area slightly exceeded that for the recoveries of the lot released 850 yards to the north. In the second experiment toads presumably returned in almost equal numbers during a two-week period from three directions, although the sample recovered from the lot released in the cleared area was actually smallest. This might be interpreted to mean that approximately half the toads in any lot or sample of the population orient themselves and return promptly, whereas the others straggle in over a long period of time. If so, the stimulus to return is stronger in the stragglers in the cleared area, or else they eventually pick up cues more readily than toads to the east or north. Further work would be required to prove either hypothesis.

Carr (1940) reports that *B. t. terrestris* breeds in Florida from March 25 to September 5, and there were toads of the species calling at the Biological Station as late as September 14 when the experiments were being conducted. The call of the male not only attracts females but serves also to direct other males to the breeding site. Goldsmith (1926) demonstrated that both sexes of the spadefoot toad, *Scaphiopus hammondii*, were stimulated by calls of the same species. He placed several individuals in an open container and gradually approached a breeding site. A mile distant the toads remained quiet, but when he was within 600 yards they became excited and active. In the experiments at the Archbold Station the presence of breeding choruses near the plaza may have enabled toads to orient themselves by means of auditory cues. There is no evidence that the hearing of toads is more acute than it is in man, although experiments and field observations suggest that toads distinguish one call from another, and are most strongly attracted by calls of their own species. When the experiments were being conducted in Florida so many species were calling simultaneously that it was impossible for the human ear to distinguish one call from another. At a distance the noise emanating from the breeding site was usually a din, although some species started calling earlier and others continued to call later in the night when the majority had ceased. The shrill voice of *Bufo quercicus* often drowned the call of *B. t. terrestris*. Consequently, it was impossible to ascertain the distance at which the call of the Carolina toad was audible to man.

Inasmuch as calls emanating from the breeding site attract both males and females of the same species it should be pointed out that during heavy downpours throughout the summer *Bufo t. terrestris* was breeding immediately west of the Archbold Biological Station. From time to time individual toads were calling from the deep, steep-sided drainage ditch east of the plaza. When there was sufficient rain to produce a foot of water in the shallow, grassy-banked ditch (not labeled on map, fig. 2) between the plaza and the railroad tracks the majority of toads were calling at that site. Later in the season when extremely heavy rains had produced large pools just west of the railroad, the ditches were abandoned and all breeding was carried on in the natural pools. Whenever there was marked breeding activity, as there was following every storm, the toads captured in the plaza were nearly all heading westward, presumably attracted by the breeding sites. Although repeated searches were made, no toads were ever found coming to the breeding sites from the cleared area west of the pools.

It seems doubtful whether many of the vast numbers of toads coming from the east had traveled great distances. They were crossing the plaza in maximum numbers on rainy nights immediately after dusk, and since they are nocturnal they could not have been traveling for prolonged periods. Virtually no toads were encountered east of some small truck gardens at the southwest corner of the property. Indeed, the bulk of the toads

appeared to be emerging from places of concealment in the gardens.

The toads used in the experiments, therefore, were probably toads that lived in the vicinity of the plaza, although many of them were obviously captured while they were merely passing through the area to which collecting activities were confined. It has been suggested that "frogs and toads may be directed to ponds because of their special sensitivity toward marsh odors or gradients of humidity" (Noble, 1931), although no one has yet ascertained precisely how a toad knows where the breeding site is located. Hormonal stimuli, coupled with seasonal hypertrophy of the gonads, which are in turn controlled by the anterior pituitary, appear to be released by the advent of rains and presumably cause the toad to seek a breeding site, but cannot affect the choice of sites. Breeding choruses constantly gain and lose members; all individuals do not arrive at the same time. Piatt (1941) reports that toads (*Bufo t. americanus*) in New York do not travel from one breeding site to another, but ordinarily leave the breeding site and do not return after mating and oviposition. Blair (1943), on the other hand, found that males of the same species in Oklahoma continued calling in one pond until mates were found, or sometimes migrated relatively short distances to another pond, and Savage (1934) states that male *Rana t. temporaria* remained behind in the pond after the female had departed, and often mated several times in one season.

Whereas several ponds variable in size and location came into existence following the heaviest rains at the Archbold Biological Station, the east side of the larger pond (figs. 3, 4, and 6) was definitely the principal breeding site. Individual toads were occasionally heard elsewhere, and until this pond was filled toads were breeding in the drainage ditch between the Station and the railroad tracks, as noted above. Under such conditions, where a single pond is the focal point for breeding, it is doubtful whether there is an appreciable amount of migration from one pond to another. The first toad to reach a pond may do so fortuitously. After he starts calling, his voice supposedly attracts other males to the same site. In many instances the same pond is selected year after year, but it does not follow that the toad upon emergence knows the direction to any particular pond. Man-made excavations filled with water at the first rain may be selected as breeding places. Such circumstantial evidence strongly suggests that toads scatter following oviposition and establish feeding sites or remain in seclusion during dry intervals. But when a heavy rain provides suitable conditions for emergence, random wandering brings one or more toads, probably those that happen to be closest, to a suitable pond and their calls attract others of both sexes. Most toads, unlike the majority of frogs, utilize temporary pools, and their generally louder calls may be of greater significance in breeding for this reason. Frogs, such as *Rana t. temporaria* whose breeding habits were described by Savage, that breed in permanent pools could continue to call for prolonged periods whereas a toad could not. This may explain the repeated matings reported by Savage.

The significance of the breeding chorus appears to have been neglected in experiments dealing with homing in toads, although it furnishes the simplest explanation for the data available from the first experiment herein reported. It will be recalled that a relatively high percentage of toads were recovered from the lot released a mile away in open, cleared land that presumably was unfamiliar territory. It is well known that sound carries farther across open areas than it does across wooded areas since trees and shrubs tend to absorb or deflect sounds. Even though it could not be proved that the voice of *terrestris* could be heard at a distance of a mile under suitable conditions, it was obvious that the chorus was more readily heard to the west of the Station than it was to the east. If it is assumed that toads liberated to the west were able to orient themselves, and moreover were attracted by the calls of their own species, the difference between the percentages of recoveries from the lots liberated to the east and north and the percentage of recoveries from lots

liberated a mile to the west is readily explained.

When released in familiar territory, a toad may rely upon visual cues to return to a favored site, as it certainly does in a maze. When liberated beyond its familiar territory but within hearing distance of a breeding chorus, it could readily utilize auditory cues and return to the breeding site. But when a toad is released in unfamiliar territory beyond the point where it can hear a breeding chorus, it does not (and probably cannot) return to a home site.

Birds, of course, are known to undertake long and successful migrations without having covered the route before, and without older birds to guide them. Aside from these migrations, ornithologists recognize two other phenomena: (1) the ability of birds to return to the home site over unfamiliar territory, even when transported hundreds of miles into regions never previously visited, and (2) the ability of birds to orient themselves and return when released in familiar territory.

The migratory movements of amphibians are limited and in most instances represent nothing more than mass movements to the breeding site; there are no reliable reports of migrations over distances exceeding a mile. The birds that are able to return to the home site over distances of hundreds of miles are, of necessity, birds with strong powers of flight. Thus they may be familiar with considerable territory even though there is seemingly little correlation between the extent of normal home ranges and the distances that various species manage to cover in order to return to the breeding site. Pigeon fanciers, as is well known, make use of training flights to familiarize their birds with increasingly greater areas. Moreover, they select the more gifted pigeons for breeding stock. By such means they have changed the habits of birds that were originally sedentary. Without training, many sedentary birds are quite unable to return to a home site and simply establish themselves at the point of release. The same birds when liberated within their familiar territory can easily return to the portion of the range previously selected.

The behavior of toads, by virtue of their relatively limited powers of locomotion, more closely approximates that of the sedentary birds. When liberated in familiar territory the toad, like the bird, may utilize visual cues. Nevertheless the data derived from the first experiment indicate that a toad can return even though it be removed a mile from familiar territory. At distances of 4 miles, in the case of *B. t. americanus*, of hundreds of miles in the case of the only *B. t. terrestris* removed more than a mile, there was apparently no incentive for toads to return or even to wander far from the site of liberation. These data are not conclusive, but the toads' failure to return when transported beyond hearing distance of the breeding choruses points to auditory cues as a factor of importance in homing.

Far more work has been done with birds than with the Amphibia in an effort to explain homing. Despite the vast amount of information amassed no indisputable explanation has been achieved. Griffin (1944) has recently reviewed the ornithological literature and summarized the more acceptable theories. He concluded in part that "many, if not all, of the homing experiments on record could be explained by assuming that when released in unfamiliar territory the birds scatter at random and explore until they find familiar landmarks," and that "the combined use of familiar landmarks, together with simple geographical, and ecological relationships such as those described . . . seems more reasonable as an explanation of homing than the postulation of a new sense organ."

Whereas it is clear that toads are incapable of traveling long distances to return to a home site, the homing behavior of toads has features in common with those observed in terrestrial birds. Vision may play a dominant role in the homing of birds, but in the nocturnal toads auditory cues offer the best explanation for the sort of homing that has been described for them. Other sensory phenomena, including vision, kinaesthetic sense, and possibly olfaction, may be factors of importance, but response to the mating call, without better evidence

to the contrary, offers the most reasonable hypothesis to account for the high percentage of returns from unfamiliar territory.

SUMMARY AND CONCLUSIONS

Two experiments with the Carolina toad (*Bufo t. terrestris*), marked by removing toes, were carried out at the Archbold Biological Station near Lake Placid in central Florida. The region, including two types of terrain, is described, the rainfall is tabulated for the four-month period during which the experiments were in progress, and there is an account of the methods used. In all, 444 toads were marked and liberated, of which 68 were subsequently recovered at the home site, defined as an area 400 yards long and 100 yards wide. The home site was adjacent to a large pond that served as the focal point for breeding activities.

In the first experiment 200 toads were liberated in six lots between the dates of May 26 and June 9. Three lots were released to the west, at distances of 100 and 300 yards, respectively, and one of them a mile distant in cleared territory not inhabited by *Bufo t. terrestris* and presumably unfamiliar to it. Three other lots were liberated at various distances from the home site in the uncleared, semi-virgin area at distances of 450 and 750 yards to the east and 850 yards to the north, respectively.

The percentages of recoveries from the three lots liberated in the semi-virgin area decreased with the distance from the home site that the toads had been liberated: 36.8 per cent at 450 yards, 20.6 per cent at 750 yards, and 16.6 per cent at 850 yards. Percentages of recoveries from lots liberated in the cleared area to the west were relatively higher in proportion to the distances than those released in the uncleared area, over 50 per cent being recovered from the lots removed 100 and 300 yards. Of greater significance was the recovery of 18.6 per cent of the lot liberated 1 mile to the west in unfamiliar territory. This percentage of recoveries is nearly as large as the percentage for the lot released only 750 yards to the east in territory that could have been familiar.

In the second experiment a series of 244 toads, taken within three days at the home site, was divided into four lots, each comprising 61 individuals. On September 1 two lots were released at points 700 yards to the east and north, respectively, in the semi-virgin area, and a third lot was removed 700 yards to the west in the cleared area. In order to estimate the number of toads that returned (in contrast to the number actually retaken), the fourth lot was liberated near the center of the area wherein they were taken. During the 14 days following their release a search of the home area was conducted every night. Toads from the three directions were recovered in equal numbers (approximately 8 per cent of each lot), whereas twice as many toads (roughly 16 per cent) were recovered in the lot liberated at the home site. These data indicate that during a two-week period about half of the toads released in the three directions managed to return to the home territory.

The validity of the sampling technique used is discussed, and the conclusion is drawn that it has greater validity for estimating the actual number of returns in homing experiments than it has for estimating the total number of individuals in a population.

The normal movements of toads are discussed and, whereas data for the population of *terrestris* used in the experiments were not secured, the published information for related subspecies and species indicates that individual toads may wander as far as 1400 yards. Thus the normal range of an individual, and hence the territory with which it is familiar, may encompass an area a mile wide.

There is no evidence that topographical knowledge, as such, plays any role in homing behavior; toads return in comparable numbers from similar distances whether the breeding site is uphill or downhill from the point of release.

Variation in the extent of familiar

territory in the home range cannot account for the difference in the results of the two experiments described. Although toads may utilize and remember landmarks for long periods, as they do in learning a maze, this ability does not explain their seasonal migrations to breeding sites and seems to be of little importance in homing behavior.

Random radial scattering from the point of release does not account for the high percentages of returns. Even though scattering may be followed by exploration and a search for suitable landmarks it would fail to explain the relatively high percentage of recoveries of toads from unfamiliar territory as opposed to lower percentages of recoveries from areas that might with greater reason be assumed to be familiar. It is improbable that more toads return from the unfamiliar territory merely because it is "more disturbing" to them than familiar territory.

Auditory cues offer the best explanation for the homing ability of toads released beyond territory familiar to them. A relatively greater percentage of toads returned from the cleared area uninhabited by *Bufo t. terrestris* than returned from the uncleared territory inhabited by, and possibly familiar to, the toads used in experiments. The calls from a breeding chorus carry farther over cleared land than they do across areas with a moderately dense vegetation that tends to absorb or deflect sounds. Hence the toads that returned from a distance of 1 mile in the cleared area to the west probably did so in response to mating calls of other males in the breeding chorus. This interpretation is in accord with the fact that toads carried beyond hearing distance of a breeding chorus make no effort to return. Within a familiar area the Carolina toad may utilize visual cues to find its way to a preferred feeding site, but when released at a distance beyond its home territory other sensory cues must be utilized if the toad is to succeed in returning.

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